

THE RELATIONSHIPS OF THE AMERICAN
BLACK-FRUITED HAWTHORNS
CRATAEGUS ERYTHROPODA, *C. RIVULARIS*,
C. SALIGNA AND *C. BRACHYACANTHA*
TO *C. SER. DOUGLASIANAE* (ROSACEAE)

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ABSTRACT

A group of black-fruited *Crataegus* (Rosaceae) from the western United States is analysed. *Crataegus erythropoda*, a species with previously poorly understood affinities, is shown to be closely related to *C. rivularis*. The affinity of *C. rivularis* and *C. saligna* is reconfirmed. The three species form a clade subtended by *C. brachyacantha* and different from the clade containing *C. douglasii* and *C. okemunii* when analyzed by PAUP using 38 morphological characteristics. *Crataegus rivularis* and *C. saligna* are lectotypified.

RESUMEN

Se estudia un grupo de *Crataegus* (Rosaceae) con frutos negros del oeste de los Estados Unidos. *Crataegus erythropoda*, una especie con afinidades pobremente conocidas, se muestra que está muy relacionado con *C. rivularis*. Se reconfirma que *C. rivularis* es también muy afín a *C. saligna*. Las tres especies forman un clado en cuya base se encuentra *C. brachyacantha* y que es diferente del clado que contiene a *C. douglasii* y *C. okemunii* cuando se analiza mediante el PAUP usando 38 características morfológicas. Se lectotipifican *Crataegus rivularis* y *C. saligna*.

Black-fruited *Crataegus* are in a substantial minority worldwide, as also in North America where perhaps seven species are black-fruited. Numerous authors have pointed out the significance of fruit color in relation to frugivore dispersal and this topic has even received a little attention for North American hawthorns (e.g. Sallabanks 1993). It is not known whether North American black-fruited hawthorns form a natural clade and without undertaking an exhaustive examination that potentially includes many red-fruited species, this fact cannot be determined. However, it had appeared to me that they fell into at least two groups, the first being all members of series *Douglasianae* (Rehd. ex Sarg.) Rehd. (this includes *C. douglasii* Lindl., *C. suksdorfii* (Sarg.) Kruschke and *C. okemunii* J.B. Phipps) together with a second group (*C. brachyacantha* Sarg. & Engelm., *C. erythropoda* Greene, *C. rivularis* Nutt. ex Torr. & A. Gray and *C. saligna* Greene) which might have

some loose interrelationship. I test this hypothesis of two clades with a cladistic analysis using 38 morphological characteristics.

Series *Douglasianae* has been the subject of a substantial amount of recent research and is more northerly than the group of species on which I focus in this paper, with a southern limit of about 43° N except in California where it is farther south. Love and Feigen (1978) showed that *C. douglasii* could hybridize with the distantly related and introduced *C. monogyna* Jacq., Brunsfeld and Johnston (1990) provided solid grounds for raising *C. suksdorfii* (Sarg.) Kruschke from a variety of *C. douglasii* to specific rank while Dickinson *et al.* (1996) contrasted the breeding systems in the 20-stamen *C. suksdorfii* and the 10-stamen *C. douglasii* to good effect. Dickinson and students are continuing their biosystematic and morphometric analyses of ser. *Douglasianae*. Recently, I described a new species, *C. okennonii*, from this group (Phipps & O'Kennon 1998). Due to this recent activity and the continuing researches of the Dickinson group on ser. *Douglasianae*, I restrict coverage of the series in this paper to the cladistic analysis merely to discover if ser. *Douglasianae* is a separate clade from the other species considered.

Here, therefore, I direct attention to the more southerly, and allopatric, component of the 'black-fruited' *Crataegi*, the group of *C. rivularis*, *C. erythropoda*, *C. saligna* and *C. brachyacantha*. The relationships of these species has always been much more controversial. *Crataegus saligna* was placed with *C. brachyacantha* by Palmer (1925), a supposition that I followed without study in the Maloid checklist (Phipps, *et al.* 1990). Then, particularly influenced by field observations, I recognized its probable affinity to *C. rivularis*, a relationship in fact explicitly noted by Greene (1896) when he described *C. saligna*. With regard to *C. erythropoda*, as recently as this year (Phipps 1999), I included this species among the western red-fruited species. Nevertheless, the existence of a few intermediate specimens noted since that paper was prepared, together with the detailed examination for this paper, and preparation of the draft description for the *Flora of North America*, showed conclusively that it was actually close to *C. rivularis*. Also recently, Welsh (1982) placed both *C. rivularis* and *C. saligna* under *C. douglasii*, a solution that I do not believe that any current student of *Crataegus* would consider tenable.

I therefore resolved to investigate the cladistic interrelationships of the North American black-fruited species and, in the cases of *C. saligna*, *C. rivularis* and *C. erythropoda*, which have never received any independent taxonomic study since their original descriptions, in contrast to ser. *Douglasianae*, to carefully characterize and typify them. In addition, *C. rivularis* and *C. saligna* are provided with detailed distribution maps for the first time. Finally, I need to comment on my cautious 'black fruited'. Species in this group either have black, purple, or burgundy fruit when fully ripe, the particular color,

and its changes during ripening, having taxonomic significance. The term 'black-fruited' in the title therefore refers to a group of related hawthorns that are predominantly, but not entirely, black-fruited at full maturity.

METHODS

An extensive sample of herbarium specimens of the taxa to be studied has been assembled by my own fieldwork in recent years, assisted by R.J. O'Kennon, together with many examples of loan specimens. As this paper is not aimed at assessing specific limits, no morphometric phenetic analysis of large samples was conducted. However, the samples were used to determine the characteristics of synthetic OTU's, one for each species, that would be analyzed by PAUP 2.4.1. The 38 characteristics used for this purpose are listed in Table 1. Distribution maps for previously unmapped or inadequately mapped species were created by Range-Mapper, a program created by the firm Tundra Vole of Fairbanks, Alaska. For this purpose, where sufficiently precise location data existed on the herbarium label this was converted into latitude/longitude coordinates accurate to the nearest minute. Files for each species were then mapped. Typification followed standard procedures. Syntypes or potential lectotypes were located, occasionally with great difficulty, and holotype or neotypes selected on the basis of goodness of fit to the protologue, citation in the protologue (if pertinent), and specimen quality, when a choice was available. No specimens are illustrated due to the existence of excellent illustrations elsewhere. The characterizations presented here of the species outside ser. *Douglasianae* are in fact somewhat detailed diagnoses because this work does not purport to be a taxonomic revision, because excellent descriptions exist elsewhere and because, in my view, they represent four well-marked species even by conservative criteria.

INTERRELATIONSHIPS

The possible and intriguing relationship between *C. saligna* and *C. rivularis* has already been suggested. If these two proved to be sister species then a new series '*Rivulares*' could be created to accommodate them. However, on reflection, it seemed that *C. rivularis* might be even closer to *C. erythropoda* on the basis of identical floral and inflorescence characteristics and fruit differing only in fully ripe color. A series that included both *C. saligna* and *C. erythropoda* is perhaps a little broader than most series in North American *Crataegus*. We need also to pay attention to Palmer's (1925) view that *C. saligna* was closely related to *C. brachyacantha* and therefore should be placed in ser. *Brevispinae* (Palmer used the *nomen nudum* *Brachyacanthae*), where I had provisionally placed it (Phipps et al. 1990) following convention and without study. *Crataegus brachyacantha* is very similar to *C. saligna* in flower and leaf characteristics

TABLE 1. Thirty-eight morphological characteristics scored for cladistic analysis.

<i>Plant, general</i>	21. Leaf teeth: glands
1. Plant habit	<i>Inflorescence</i>
2. Bark type	22. Flower: number
3. Branch arrangement	23. Pedicel: pubescence
<i>Thorns and Twigs</i>	24. Anthesis time
4. Thorns: indeterminate present?	<i>Flower</i>
5. Thorns: length	25. Diameter
6. Thorns: curvature	26. Calyx lobes: margins
7. Thorns, color: browns	27. Stamen: no.
8. Thorns, color: gray	28. Anther: color
9. Twigs, 1 yr old, color: browns	29. Style: number
10. Twigs, 1 yr old, color: gray	<i>Fruit</i>
<i>Leaf</i>	30. Fruit: color, month before full ripeness
11. Lamina: length	31. Fruit: color at full ripeness
12. Lamina: length/breadth	32. Fruit: shape, 1
13. Lamina: position of widest part	33. Fruit: shape, 2
14. Lamina: venation, number	34. Fruit: pubescence
15. Lamina: veins to sinuses	35. Fruit: calyx orientation
16. Lamina: lobe number	36. Fruit: length (height)
17. Lamina: lobe shape	37. Pyrenes: lateral faces
18. Lamina: max. sinus depth (LH)	<i>Autumnal foliage</i>
19. Lamina: abaxial pubescence, young	38. Color
20. Petiole: glands	

but differs greatly in the thorns (curved, ≤ 1.5 cm long), color of overmature inflorescence (yellowish orange), fruit size (generally larger), smooth lateral faces of the pyrenes, and lack of copper-colored bark. Also Welsh had made both *C. saligna* and *C. rivularis* varieties of *C. douglasii*, in what seemed to me to be an untenable association. It therefore seemed pointful to conduct a numerical taxonomic study to throw light on these contrasting possibilities and to establish whether any of these taxa were especially close to members of ser. *Douglasianae*.

For this, I scored 38 characters (Table 1) for 9 synthetic OTUs, one for each species, which included all the black-fruited *Crataegus* species that are the particular subjects of this paper (*C. saligna*, *C. rivularis*, *C. erythropoda* and *C. brachyacantha*) plus *C. douglasii* s.s., *C. suksdorfii* and *C. okemnonii* of ser. *Douglasianae* as well as the red-fruited outgroups *C. mollis* (Torr. & A.Gr.) Scheele and *C. monogyna* Jacq.

Using PAUP 2.4.1, *C. erythropoda* and *C. rivularis* are shown to be sister species in the three shortest trees (Fig. 1). The *douglasii* group, consisting of *C. douglasii* and *okemnonii*, always formed one sub-clade while *C. brachyacantha*, *C. saligna*, *C. rivularis* and *C. erythropoda* always formed another in all shortest cladograms. However, *C. saligna* and *C. brachyacantha* were by no means very close in these cladograms although *C. rivularis* and *C. erythropoda* were

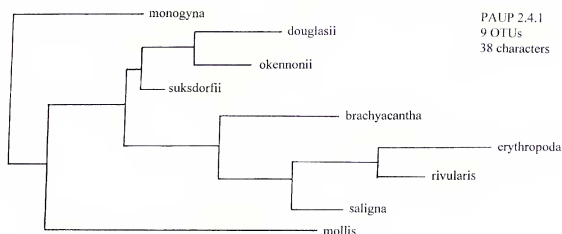


FIG. 1. Cladogram of North-American black-fruited *Crataegi* created by PAUP using 38 morphological characters.

shown in all analyses to be sister species. The two unpublished trees only differ in the location of *C. suksdorfii* which is either basal to *C. douglasii* / *okennonii* (published tree), basal to (B(Sa(R,E))), using their epithet abbreviations, in one unpublished tree or basal to both (D,O) and (B(Sa(R,E))) in the other.

The union of all seven black-fruited species inside the red-fruited outgroups *C. mollis* and *C. monogyna* does not, however, indicate that the black-fruited group is monophyletic. An analysis using all the red-fruited species would be required to generate such a finding and that is not the function of this exercise. Rather, it is to locate the position of *C. erythropoda*, *C. rivularis*, *C. saligna* and *C. brachyacantha* relative to the immediate *C. douglasii* group. The cladogram endorses the view that neither *C. saligna* nor *C. rivularis* are part of the species *C. douglasii*. The following key summarizes the differences among the four species in *rivularis* clade.

KEY TO *RIVULARIS*-CLADE OF BLACK AND BURGUNDY-FRUITED *CRATAEGUS*

1. Stamens 20; anthers cream; flowers 10–12 mm diam.
 2. Thorns 1–1.5 cm long, decurved, grayish; twigs grayish; overmature flowers orange-yellow; nutlets with lateral faces plane *C. brachyacantha*
 2. Thorns 2–4 cm long, straight, black; twigs copper-colored; overmature flowers white to dirty white; nutlets with lateral faces pitted *C. saligna*
1. Stamens 10; anthers pink; flowers 15–17 mm diam.
 3. Leaves essentially unlobed, usually more than 2 times as long as broad, widest near the middle; fully ripe fruit black *C. rivularis*
 3. Leaves evidently about 3-lobed per side; usually ca. 1.5 times as long as broad, usually widest in the basal third; fully ripe fruit usually burgundy *C. erythropoda*

TAXONOMIC AND NOMENCLATURAL NOTES ON INDIVIDUAL SPECIES

CRATAEGUS ERYTHROPODA—Characterization

Crataegus erythropoda Ashe, North Carolina Agric. Exp. Sta. Bull. 175:113. 1900.

Crataegus bakeri Greene, nomen nudum

This species has been described, illustrated and mapped in my recent paper (Phipps 1999) where it was entered into a new monotypic series, *Cerrones*. J.B. Phipps, on account of its distinctness from other red-fruited species. *Crataegus erythropoda* may be briefly characterized by its ovate-rhombic, ± glabrous, shallowly-lobed, smallish leaves; glabrous inflorescences with 10-stamen flowers having pink-purple anthers; suborbicular fruit which is burgundy at maturity (I have never once seen 'orange' as described in the protologue by Ashe (1900) and Holmgren (1997)); shiny coppery bark on 2–5 cm thick stems and thorns mainly 2–4 cm long. *Crataegus erythropoda* occurs in sites with groundwater available, or otherwise mesic, mainly in intermountain Colorado and adjacent New Mexico, where it is quite common. Holmgren (1997) also records it from eastern Utah and northeastern Arizona. The 'orange' fruit color cited may refer to immature fruit since the type was collected in August, but I have not myself seen this color even in mid-August. *Crataegus erythropoda* has presented no serious problems in delimitation or recognition though its relationships have been hitherto obscure. See the protologue (Ashe 1900) for another full description. Interestingly, Palmer (1925) assigned *C. erythropoda* to ser. *Douglasianae*, an idea taken up by no-one else, but nevertheless the closest approximation to date. Observations made for this paper indicate that at anthesis *C. erythropoda* is almost indistinguishable from *C. rivularis* in floral/inflorescence characteristics. Significant differences in leaf shape and ripe fruit color exist, however, as indicated in the key.

A specimen of Greene's from the Lower Cimarron River, Colorado (NDG), collected in 1896 and labelled '*C. bakeri*', a name never published, is actually a perfectly adequate specimen of *C. erythropoda* Ashe.

CRATAEGUS RIVULARIS—Synonymy, Characterization and Typification

Crataegus rivularis Nutt. ap. Torr. & A. Gray, Fl. N. Amer. 1:464. 1840.

Crataegus douglasii Lindl. var. *rivularis* (Nutt. ap. Torr. & A. Gray) Sarg., Gard. & Forest 4:81. 1902.

As with *C. erythropoda*, there have not been serious problems in taxon recognition or delimitation although some floristic authors have followed Sargent (1889) in relegating *C. rivularis* to varietal rank under *C. douglasii*.

Crataegus rivularis is a locally common, even locally abundant, species of intermountain USA, found in many locations in this generally dry area where there is a high water-table. I map this widespread species (Fig. 2) which

occurs from southern Idaho to northern New Mexico and from south-central Utah east to the Rocky Mountains. It reaches 6–7 m in favorable sites where it may form extensive thickets. The bark of 2 cm diameter branches is copper-colored like *C. erythropoda* and the generally fine thorns are mainly 2.5–4 cm long. The normally elliptic leaves are tapered at each end, subglabrous, 4–6-veined and quite unlobed on short-shoots, being beset with many sharp, forward-pointing fine marginal teeth. The glabrous inflorescence bears large 10-stamened flowers with pink anthers and can hardly be differentiated from that of *C. erythropoda*. The numerous, often large, suborbicular fruit pass through a striking deep reddish-burgundy color to deep purple and finally black. See also Sargent (1890) for a detailed characterization and excellent plate by Faxon. Intermediates with *C. douglasii* are not known and *C. rivularis* is essentially allopatric with that more northern species which facts reinforce the findings of the cladistic analysis. However, because Welsh (1982), Holmgren (1997), and Sargent (1889, 1890) have included *C. rivularis* in *C. douglasii*, I would like to emphasize their distinction with the following key couplet.

1. Thorns fine, little recurved, usually 2.5–5 cm long; bark of 1–2 cm diam. branches shiny coppery brown; flowers 14–18 mm diameter, calyx lobes 5–8 mm long, long-attenuate from a broad base; leaves narrow elliptic, unlobed or rarely with 1–2 very small lobes per side, tapered at both ends, acute to acuminate at the apex, the venation semi-camptodromous; fruit subglobose, 11–14 mm diam., crimson-lake ripening to shiny black *C. rivularis*
1. Thorns stout, often recurved, usually 1.5–3 cm long; bark of 1–2 cm diam. branches tan to gray-brown; flowers 12–15 mm diam., calyx lobes 3–4 mm long, narrow-triangular from a broad base; leaves much broader, most commonly broad elliptic to narrow-obovate in general shape, usually lobed (unlobed in rare narrow-leaved specimens), the venation clearly craspedodromous except in rare narrow-leaved specimens, usually obtuse to subacute at the apex; fruit generally ellipsoid, usually ≤ 9 mm diameter, ripening dull purple to purple-black or black, generally with rather strong bloom *C. douglasii*, s.s.

The suite of differences is so large, together with the lack of intermediates and different distribution, that one cannot reasonably place *C. rivularis* in the same species as *C. douglasii*.

In making *C. rivularis* a variety of *C. douglasii* Sargent's overall understanding of this taxon was poor, illustrated by his providing (1890) an inaccurate range extension from northwestern California to Puget Sound and his statement, "usually a low intricately branched.....shrub." This perhaps helps to explain the cautious rank chosen by Sargent, a notorious splitter by modern criteria.

Crataegus rivularis has not been typified, therefore, I lectotypify it here. The type description for *C. rivularis* (Torrey & Gray 1843) is of characteristic brevity and imprecision for the period and might at first sight refer to

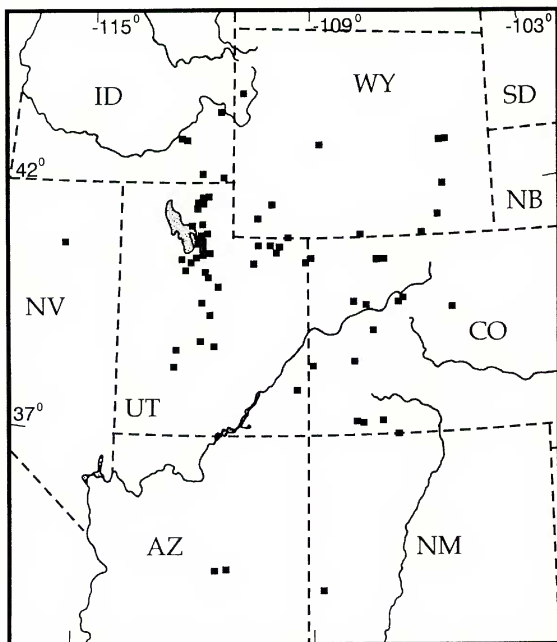


FIG. 2. Distribution of *C. rivularis* Nutt. ap. Torrey and A. Gray from collated herbarium records.

C. douglasii or even *C. saligna*, as well as to the taxon normally associated with the name.

The protologue for *C. rivularis* cites "Oregon, rivulets in the Rocky Mountains" as the type area with Nuttall as collector. It is hard to know exactly where this is, because of the extensive nature of the Oregon Territory in 1843. What we call *C. rivularis* today is a distinct, well-collected taxon with a well-established range (Fig. 2) which just reaches southern Idaho, part of which is an acceptable area for "Rocky Mountains." Putative syntype ma-

terials of *C. rivularis* from BM, GH and PH were borrowed in order to lectotypify this species.

Of the two PH specimens sent (both on the same sheet) one (on the right-hand side) can be rejected directly as it is a Canby-collected *C. douglasii* from 1873, while the left-hand specimen, labelled 'Rocky Mountains', is a leafy twig without reproductive material that requires comparison with the protologue. Both the BM and GH sheets have specimens collected by Nuttall that are a reasonable match for the somewhat poor description in the protologue and are clearly the same species as each other. In view of the indifferent quality of the protologue and the consequence that a species other than what is conventionally called *C. rivularis* might have been described, I provide in Table 2 critical comparisons between the protologue and putative types (cols. 1, 2), between the protologue and *C. douglasii* (col. 3) and between the protologue and standard interpretation of *C. rivularis* (col. 4).

Several points in the protologue cannot be assessed from the putative syntypes from BM and GH. These are the arborescent nature of the plant (not recorded on the collection label) and flowering characteristics (the putative syntypes are post-flowering). Also, Nuttall in describing the leaves as "ovate, obovate" poses something of a problem, as these are not terms that we would apply today to the putative syntype leaves, which are clearly nearer to narrowly elliptic. In fact, in examining many protologues for *C. series Coccineae* drawn up by C.S. Sargent in the first and second decades of this century, I have observed that "ovate" is almost a generic leaf-shape. In my opinion, having also examined many other *Crataegus* type descriptions from the nineteenth century and earlier, the term "ovate" was not used with its present precision and therefore, with regard to leaf-shape, the protologue may be said to describe the material of the putative syntypes in question with adequate accuracy for the period. The other characters match the protologue. As to the PH putative syntype (col. 2), the matches between it and the protologue are so few as to be almost meaningless. Moreover, the specimen possibly belongs to *C. crus-galli*, as previously stated by Eggleston in an annotation on the sheet, but this is a species never found in the Rocky Mountain area. However, the specimen also resembles *C. saligna*, but because it is sterile, conspecificity is uncertain. The final two columns in the table compare the protologue with typical *C. douglasii* and what is normally called *C. rivularis* (alternatively *C. douglasii* var. *rivularis*). Because *C. douglasii* has lobed leaf-blades and "short" thorns, whereas *C. rivularis* has longer thorns and unlobed leaves, the latter constitutes the better match for the protologue. Thus, the choice of lectotype lies between inadequate vegetative material of what is possibly *C. saligna* at PH and adequate specimens clearly representing what is normally called *C. rivularis* at BM and GH. Therefore, I lectotypify

TABLE 2. Comparison of protologue characteristics with putative syntypes of *C. rivularis* (see text) and with plants of *C. douglasii* and *C. rivularis*.

protologue characteristics	match for putative syntypes at BM,GH	match for putative syntype at PH	match for <i>C.</i> <i>douglasii</i>	match for <i>C.</i> <i>rivularis</i>
<i>Arborescent</i>	?	?	+	+
<i>Nearly glabrous</i>	+	+	+	+
<i>Not glandular</i>	+	+	+	+
<i>Leaves</i> - ovate or obovate	?, ?	?, ?	+, +	?, ?
- obtuse or sometimes acute	+	+	+	+
- simply or somewhat incisely serrate	+	+	•	+
- attenuate into a short petiole	+	+	+	+
<i>Thorns</i> - "spines" long	+	?	•	+
<i>Corymb</i> - many flowered	?	?	±	±
- glabrous	?	?	us	+
- flowers small	?	?	+	+
- segments of calyx obtuse and very short	±	?	+	±
<i>Fruit</i> - black	?	?	+	+
?	= cannot determine a match			
+	= perfect match			
±	= reasonable match			
us	= usually a match			
•	= not a match			

C. rivularis with the Nuttall specimen "Rocky Mountains" (holotype BM; isotype GH) and retain the usual interpretation of this taxon.

CRATAEGUS SALIGNA—Synonymy, Characterization and Typification
Crataegus saligna Greene, Pittonia 3:99. 1896.

Crataegus wheeleri A. Nelson, Bot. Gaz. 34:369. 1902.

Crataegus douglasii Lindl. var. *duchesneensis* S.L. Welsh, Great Basin Naturalist 42:9. 1982.

Crataegus saligna is a medium-sized to large thicket-forming bush growing along streams and other locally moist areas in intermountain Colorado and northeastern Utah (Fig. 3). Its range is the most restricted of the four species dealt with in this paper. In many respects it is like *C. rivularis* but it has smaller leaves, thorns, flowers and fruit and 20 cream instead of 10 pink anthers. The fruit is more fully black (darker than *C. rivularis* when sub-ripe in late August) and the leaf-teeth are quite different from *C. rivularis*, being small, numerous and obtuse, rather than longer and sharp. Moreover

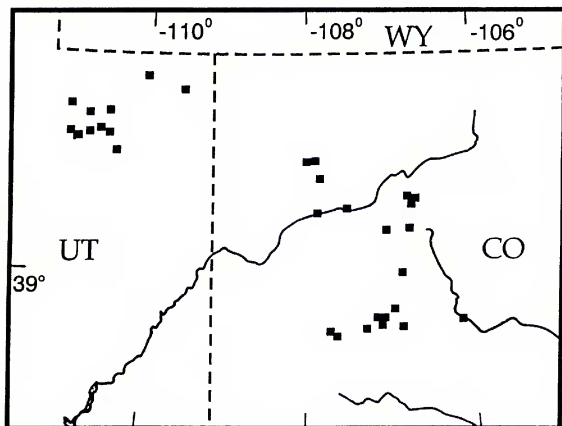


FIG. 3. Distribution of *C. saligna* Greene from collated herbarium records.

there are usually 6–9 lateral veins on one side of a leaf, compared to 4–5 in the much larger leaf of *C. rivularis*. Indeed, the leaves are remarkably similar to those of *C. brachyacantha*. *Crataegus saligna* has sometimes been confused with *C. douglasii* from which it has even more differences than *C. rivularis* and it was erroneously called *C. douglasii* var. *duchesnensis* by Welsh (1982). It is similar to *C. rivularis* in its coppery bark on 2–5 cm diameter branches, and slender, \pm straight thorns usually 2–4 cm long [except recurved and 0.75–1.5 cm long in *W.W. Robbins* 6972 from Newcastle, Colo. (COLO)], narrow leaves, intermountain distribution and similar habitat.

Crataegus saligna was described by Greene (1896) from the Lower Cimarron River, Colorado, without citation of type material, a situation that has not been remedied to date. My search for potential lectotype material involved the main Greene herbarium at Notre Dame University, Indiana (NDG), WIS and NA where remnants of the remainder of Greene's herbarium had been dispersed from LCU, and CAS, COLO, NY, UC, and US. Only one herbarium generated a putative lectotype, the specimen being *E.L. Greene s.n.*, Colo., Cimarron, 31 Aug 1896 (NY). I therefore lectotypify *C. saligna* by this specimen. Fortunately, the type description of *C. saligna* is entirely adequate for species recognition, such that this taxon has become a well-accepted element in the Colorado flora (Harrington 1964; Weber & Wittmann

1992). Sargent (1902) provided a more extensive description of *C. saligna*, together with the citation of specimens dating back to 1845 and a fine illustration by Faxon.

Crandall's 1896 collection of *C. saligna* (at RM) from the Lower Cimarron River also became a potential lectotype for this species because the Lower Cimarron River, Greene's type location for *C. saligna*, enters the Black Canyon of the Gunnison. However, there is no indication that Crandall's specimen was ever studied by Greene, and therefore it is rejected for this purpose.

Wheeler also collected several hawthorn specimens from the same area, but in 1898, too late to be lectotype material of *C. saligna* but which it is convenient to comment on here. From among these, Aven Nelson (1902) described *C. wheeleri* which I lectotypify by *H.N. Wheeler* 523, Black Canyon of the Gunnison (RM). As this is identical to *C. saligna*, *C. wheeleri* becomes a synonym of that species.

Complicating the taxonomic picture was S.L. Welsh's description (Welsh 1982) of a new variety of *C. douglasii*, var. *duchesnensis* S.L. Welsh, from northeastern Utah. From the type description, though very brief, this new taxon appeared to me to resemble *C. saligna* rather than *C. douglasii*. Loan of relevant material from BRY proved this suspicion to be correct, consequently *C. douglasii* Lindl. var. *duchesnensis* S.L. Welsh is here synonymized under *C. saligna*. Also, some of Welsh's specimens annotated as his new variety of *C. douglasii* proved to be *C. rivularis* and I therefore supply hereunder a list of Utah specimens cited by Welsh (1982) as *C. douglasii* var. *duchesnensis* that I identify as *C. saligna*:

UTAH: Duchesne Co.: 5 mi N of Fruitland, 21 Jun 1965, *J. Brotherson* 508; 5 mi NW of Hannah, 17 Aug 1965, *K.S. Erdman* 2522; T15 R6W Sec. 36, 9 Jun 1976, *Dennis J. Hansen s.n.*; 24 km NW of Duchesne, along Utah Hwy. 35, 10 Sep 1970, *S.L. Welsh, N.D. Atwood and G. Moore* 10928 (HOLOTYPE). Uintah Co.: Merkley Park, 18 May 1963, *S.L. Welsh & G. Moore* 1948.

These records, and others of my own generated by this discovery, represent quite a significant range extension for *C. saligna*, a species hitherto known only from intermountain Colorado. I therefore offer what I believe to be the first published range map (Fig. 3) of *C. saligna*.

CRATAEGUS BRACHYACANTHA Sarg. & Engelm.—Characterization
Crataegus brachyacantha Sarg. & Engelm., Bot. Gaz. 7:128. 1882.

Crataegus brachyacantha lies among the select group of hawthorns without synonymy, this fact alone attesting to its distinctiveness. It is one of the largest North American hawthorns, occasionally reaching 14 m tall, though it is more usually a bush or small tree at maturity 4–8 m tall. It occurs naturally throughout Louisiana and the adjacent parts of all surrounding states reaching its best growth on moist bottomlands. The twigs are beset

with few to numerous very short (ca. 1 cm long) recurved thorns, unique in *Crataegus* to my knowledge. The short-shoot leaves are elliptic, unlobed, very glossy, glabrous with numerous secondary veins and crenate margins. They resemble the leaves of *C. saligna* and color brilliantly in autumn. The multi-flowered inflorescence is glabrous and turns orange-yellow when over-mature, also apparently unique in *Crataegus*. The small flowers have 20 stamens. The fruit, dead-black at full maturity, is covered by a dense bloom before the bloom is abraded, and together with a more purple-black sub-mature skin, the fruit may look 'blue', hence the vernacular name 'blueberry haw'. The fruit is somewhat bitter and has five plane-sided nutlets. Full descriptions and illustrations may be found in Phipps (1998) and Sargent (1902). The species is also mapped in detail in Phipps (1998). A white-fruited variant, unique to *Crataegus* in this respect, was seen in 1922.

There is no problem in delimiting this species and it has never been thought to be especially closely related to, or a part of, *C. douglasii*.

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REFERENCES

- ASHE, W.W. 1900. *Crataegus erythropoda*. North Carolina Agric. Exp. Sta. Bull. 175:113.
- BRUNSFELD, S.J. and E.D. JOHNSON. 1990. Cytological, morphological and phenological support for specific status of *Crataegus suksdorfii* (Rosaceae). *Madroño* 37:274–282.
- DICKINSON, T.A., S. BELAOUSSOFF, R.M. LOVE, and M. MUNIYAMMA. 1996. North American black-fruited hawthorns (*Crataegus* sect. *Douglasii* Loud.): 1. Variation in floral construction, breeding system correlates and their possible evolutionary significance. *Folia Geobot. Phytotax.* 31: 355–371.
- GREENE, E.L. 1896. *Crataegus saligna* n. sp. *Pittonia* 3:99.
- HARRINGTON, H.D. 1964. Manual of the plants of Colorado - a biodiversity baseline, 2nd ed. Sage Books, Denver, Colorado.
- HOLMGREN, N.H. 1997. *Crataegus*. In: A. Cronquist, N.H. Holmgren and P.K. Holmgren. Intermountain Flora 3A, pp. 154–158.
- KRUSCHKE, E.P. 1965. Contributions to the taxonomy of *Crataegus*. Milwaukee Public Mus. Public. Bot. 3:1–273.
- LOVE, R. and M. FEIGEN. 1978. Interspecific hybridization between native and naturalized *Crataegus* (Rosaceae) in western Oregon. *Madroño* 25:211–217.
- NELSON, A. 1902. *Crataegus ucheeleri*, n. sp. *Bot. Gaz.* 34:369.
- PALMER, E.J. 1925. Synopsis of North American *Crataegus*. *J. Arnold Arbor.* 6:5–128.
- PHIPPS, J.B. 1998. Synopsis of *Crataegus* Series *Apiifoliae*, *Cordatae*, *Microcarpae* and *Brevispinae* (Rosaceae subfam. Maloideae). *Ann. Missouri. Bot. Gard.* 85:475–491.

- PHIPPS, J.B. 1999. Introduction to the red-fruited *Crataegus* of western North America. *Canad. J. Bot.* 76:1863–1899.
- PHIPPS, J.B. and R.J. O'KENNON. 1998. Three new species of *Crataegus* (Rosaceae) from western North America: *C. okenonii*, *C. okanagenensis* and *C. phippsii*. *Sida* 18:169–181.
- PHIPPS, J.B., K.R. ROBERTSON, P.G. SMITH, and J.R. ROHRER. 1990. A checklist of sub-family Maloideae (Rosaceae). *Canad. J. Bot.* 68:2209–2269.
- SARGENT, C.S. 1889. *Crataegus douglasii* Lindl. var. *rivularis*, n. var. *Gard. & Forest* 2:401.
- SARGENT, C.S. 1890. The *Silva* of North America, IV:87–88, t. 176. Houghton Mifflin, Boston, Mass. and New York, N.Y.
- SARGENT, C.S. 1902. The *Silva* of North America. Suppl. XIII: 37–38, t. 636. Houghton Mifflin, Boston, Mass. and New York, N.Y.
- SALLABANKS, R. 1993. Fruiting plant attractiveness to avian seed dispersers: native vs. invasive *Crataegus* in western Oregon. *Madroño* 40:108–116.
- TORREY, J. and A. GRAY. 1843. *Crataegus rivularis*. In: *A Flora of North America* 1:464. New York, Wiley & Putnam.
- WEBER, W.A. and R.C. WITTMANN. 1992. Catalog of the Colorado Flora. Univ. of Colorado Press, Niwot.
- WELSH, S.L. 1982. *Crataegus*. In: *Utah Flora, Rosaceae*. *Great Basin Naturalist*. 42:9–10.